

POLLINATOR SHARING BY THREE SYMPATRIC MILKVETCHES, INCLUDING THE ENDANGERED SPECIES *ASTRAGALUS MONTII*

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ABSTRACT.—Insects visiting flowers of the endangered Heliotrope milkvetch, *Astragalus montii*, were compared with those visiting two common sympatric congeners, *A. kentrophyta* and *A. miser*, on three sites on the Wasatch Plateau of central Utah for 2 yr. We recorded 27+ species of bees, most of which were uncommon, visiting the three species. All three species were primarily visited by native bees of the genera *Osmia* (15 species) and/or *Bombus* (4 species). Most *Osmia* species visited the three species of *Astragalus* indiscriminantly; bumblebees preferred *A. miser* and avoided *A. montii*. Our hypothesis that *A. montii* flowers would receive fewer total bee visits and be visited by fewer bee species than their common congeners was rejected: *A. montii* was intermediate to the two common species in its attractiveness to bees. Also rejected was our hypothesis that the greater similarity between *A. montii* and *A. kentrophyta* in flower size, flower morphology, and microhabitat would be associated with greater similarity of flower visitors than either had with *A. miser*. The data suggest that, rather than competing with each other for pollinators, the three species of *Astragalus* facilitate each other's visitation rates.

Key words: *Astragalus*, *milkvetch*, *endangered plant*, *reproduction*, *pollination*, *facilitation*, *bee diversity*, *conservation*, *Fabaceae*, *Osmia*.

Many insects such as dipterans and lepidopterans use flowers only as fuel stations (Elton 1966); they collect nectar and burn it as they search for suitable spots to lay eggs. Such insects may merely pass through areas where flowers are sparse. Bees, in contrast, are central-place foragers (Orians and Pearson 1979) that must consistently reap profits in both nectar and pollen, for they forage not simply to underwrite their own movements, but to provide food to rear their progeny as well (Stephen et al. 1969). Because bees are under strong, selective pressure to be profitable foragers, they are attracted to dense patches of flowers (Heinrich 1976, 1979, Thomson 1982). Bumblebees, for example, quickly recognize and exploit particularly rewarding flower patches (Heinrich 1976, 1979); other bees probably do so also.

Density-dependent foraging behavior by bees has important implications for certain rare plants. Rabinowitz (1981) distinguished seven types of rarity in plants using the following three criteria: (1) local abundance, (2) habitat specificity (narrow or wide), and (3) geographic range (large or small). Those species with both narrow habitat specificity and small local populations (regardless of geographic range) are

sparse and likely to attract foraging bees only incidentally. We expect such species to be pollinator-vulnerable and, therefore, to be highly self-compatible and perhaps primarily self-pollinating (Karron 1987). It is less clear whether plants in other categories of rarity, especially endemics (Rabinowitz 1981, Kruckberg and Rabinowitz 1985), are also pollinator-vulnerable. Endemics have narrow habitat specificity but may be locally abundant.

One such endemic, the rare Heliotrope milkvetch, *Astragalus montii* Welsh, is limited to a few isolated populations in limestone gravel outcrops on the Wasatch Plateau of central Utah at about 3350 m. There it grows with two common congeners, *A. kentrophyta* var. *tegetarius* (S. Wats.) Dorn, hereafter *A. kentrophyta*, and *A. miser* var. *oblongifolius* (Rydb.) Cron., hereafter *A. miser*. In all three species, seed production requires, or is increased by, pollinator visits to flowers (Geer and Tepedino 1993). Information on the identity and biology of these pollinators is important, for *A. montii* occurs on rangelands that are grazed by domestic livestock and sprayed with insecticides to control grasshoppers. Successful management of this rare species requires

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knowledge of how such spraying may affect its pollinators.

In this report we compared composition and abundance of pollinator fauna of *A. montii* with those of its two sympatric congeners. Because there may be wide variation in a species' pollinators between years and sites (Tepedino and Stanton 1981, Herrera 1990, Eckhart 1992), we censused pollinators of *A. montii* and its congeners for 2 yr at three sites. We hypothesized that *A. montii* would (1) attract fewer individual pollinators, (2) have lower pollinator species diversity than its two common congeners, and (3) share more species of flower visitors with *A. kentrophyta* than with *A. miser* because similarity in plant and flower size, flowering time, and microhabitat is greater with the former than with the latter.

SPECIES AND STUDY AREAS

All three species of *Astragalus* are small perennial herbaceous legumes. *A. montii* is restricted to three mountaintops on the Wasatch Plateau in central Utah. Although Isely (1983) proposed that *A. montii* be reduced in status to a variety of *A. limnocharis* Barneby, it was listed as endangered under the Endangered Species Act in 1987 as *A. montii* and remains so (Anonymous 1991). Therefore, we refer to this taxon as *A. montii*.

A. kentrophyta and *A. miser* are widespread species that occur with *A. montii* at three sites on two of the mountains; the third mountain is less accessible and was not included in the study. *A. kentrophyta* is widespread and abundant in the Rocky Mountains, mostly between 2280 and 3650 m. *A. miser*, one of the most common species of *Astragalus* in the Rocky Mountains, is locally abundant from sagebrush foothills to the spruce-fir belt (Barneby 1989). The three species co-occur at 3250 to 3350 m in an Engelmann spruce (*Picea engelmannii* Parry)/subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) community. *A. montii* and *A. kentrophyta* are intermingled in limestone gravel outcrops where *A. miser* is found only occasionally. *A. miser* is most abundant nearby where soil is deeper and less rocky. *A. montii* and *A. miser* occur at similar local densities on Heliotrope Mountain ($9.3 \pm 0.1/m^2$ and $12.6 \pm 8.3/m^2$; Geer unpublished data). There are fewer *A. kentrophyta* ($2.6 \pm 0.8/m^2$; Geer unpublished), but individuals cover more ground

than do those of its congeners. The three species overlap in bloom time for about 3 wk (Fig. 1).

Heliotrope milkvetch is a subacaulescent plant 1–5 cm tall that arises from a branched caudex. Flowers are deep purple with white wingtips. There may be a dozen to a hundred or more flowers (7.8 ± 1.5 mm long, $N = 10$; Geer unpublished) per plant, two to eight per raceme (Barneby 1989). It does not appear to reproduce vegetatively (personal observation). In 1989 and 1990 *A. montii* commenced flowering with final snowmelt beginning as early as June and continuing for about 4 wk until mid-July (Fig. 1).

The common species *A. kentrophyta* started to flower approximately 1 wk before *A. montii* and continued to flower through early August. It is prostrate, with stems that fork repeatedly and closely to form low convex cushions covered with small blue-white to purplish flowers (6.6 ± 1.2 mm long, $N = 10$; Geer unpublished), only two per raceme (Barneby 1989).

The other common congener, *A. miser*, commenced flowering 1–2 wk after *A. montii* and continued flowering until September. It is taller (2–20 cm) than *A. montii* or *A. kentrophyta*. Flowers are larger (11.4 ± 1.4 mm long, $N = 11$; Geer unpublished) and vary in number per raceme (3–15; Barneby 1989) and in color; flowers may be white, pink, or lavender.

All *Astragalus* species have papilionaceous blossoms composed of a showy standard or banner petal, a keel that protects the joined stamens and pistil, and two wings that, along with the keel, typically serve as a landing platform (Kalin Arroyo 1981). To trip *A. miser* flowers, bees land on the keel and force their way under the banner (personal observation) as they do for other species of *Astragalus* (Green and Bohart 1975, Faegri and van der Pijl 1979). Visitors to *A. montii* or *A. kentrophyta* spread the wing petals with their midlegs and take nectar, or comb pollen from the anthers to their abdominal pollen baskets with their forelegs (personal observation). Stylar hairs (termed a brush mechanism) aid in the collection of pollen by transporting it from the keel outward (Kalin Arroyo 1981).

Sexual reproduction by *A. miser* and *A. kentrophyta* requires insects to transfer pollen; *A. montii* is capable of unassisted self-pollination (autogamy). However, fruits produced autogamously by *A. montii* may be inferior in

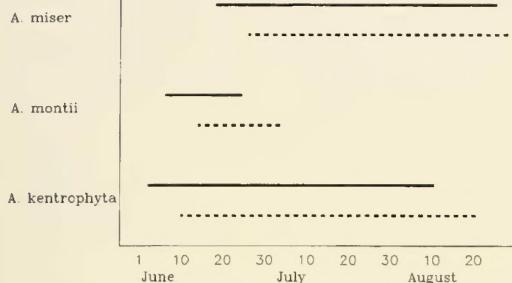


Fig. 1. Blooming dates for three co-occurring species of *Astragalus* at the SSH site. Solid line = 1989; dashed line = 1990.

quality to those produced by geitonogamous or xenogamous hand pollinations, or open-pollinated control treatments (there are fewer seeds per fruit and seeds are smaller; Geer and Tepedino 1993). Thus all three species probably benefit from insect visitation.

METHODS

Insect visitors were collected for about 3 wk in 1989 and for 2 wk in 1990 at the following three sites, starting when *A. montii* was in peak bloom: the head of Mill Stream on Ferron Mountain (HMS), south side of Heliotrope Mountain (SSH), and east end of Heliotrope Mountain (EEH). In 1990 collections from all three *Astragalus* species were made only at the SSH site because only two insect collectors were available instead of four, as in 1989. We concentrated on the SSH site in 1990 to make the number of collector hours there equivalent to the 1989 effort. In 1990 visitors to *A. kentrophyta* were collected at the SSH and HMS sites, and visitors to *A. miser* were collected at the SSH and EEH sites. Following are approximate direct distances between sites: HMS to SSH = 3.6 km, HMS to EEH = 2.4 km, and EEH to SSH = 1.2 km.

Pollinators were collected with a standard butterfly net and killed in cyanide jars. Cold temperatures, strong winds, and frequent precipitation (snow and rain) prohibited pollinators from flying during all but brief windows of calm, sunny weather, so opportunistic collection was necessary to ensure an adequate sample size. Collections were made from all three species contemporaneously, whenever weather permitted (i.e., temperatures >13°C, little

wind, and no precipitation). Initially, sight identification of some taxa was attempted so as to reduce impact on the pollinator community. It soon became obvious that it was impossible to identify *Osmia* and other individuals without laboratory examination. Subsequently, all flower visitors were collected whenever possible. Few insects other than bees visited the flowers.

Diversity of bee visitors to each *Astragalus* species was calculated using Simpson's diversity index, $D = 1 - \sum_{i=1}^s (P_i)^2$, where P_i = the proportion of individuals that belong to each bee species (Southwood 1978). Simpson's index gives little weight to rare species and more weight to common ones. Similarity of the bee fauna visiting *Astragalus* species was estimated using Czekanowski's similarity index: $C_s = NJ/(a+b+\dots+n)$, where N is the number of plant species being compared, J is the number of bee species shared by those plant species, and a, b, \dots , are the total number of bee species visiting each plant species (Southwood 1978). C_s is based on species presence alone. We also calculated C_i , which adjusts for the number of individuals per species (Southwood 1978). The indices range from 0 (no similarity) to 1.0 (complete similarity). They were calculated between pairs of species and among all three species.

Probable pollinators of the three *Astragalus* species were ascertained by examining flower visitors and recording areas of their bodies on which pollen was found. Specimens were then relaxed and pollen was removed using an insect pin or by dabbing it with acid-fuchsin gel (Beattie 1971). The pollen was placed on a glass slide with acid-fuchsin gel, warmed until liquid, and a cover slip applied (modified from Faegri and Iverson 1964). One slide per leg or two slides per abdomen were made for each insect. All slides were viewed at 100X magnification and the pollen compared to a pollen reference collection of species in bloom at the study sites.

RESULTS

Bees were scarce at the study sites in both years (Table 1, Appendices I, II). Bee visitors per plant species ranged from about 0.5 to just over 3 per hour, a small number considering that many flowers of each species were being monitored. Bee numbers were higher in 1990;

TABLE 1. Number of person hours spent collecting and number of bee individuals collected or observed visiting flowers of *Astragalus montii* (Asmo), *A. kentrophyta* (Aske), and *A. miser* (Asmi) at three sites on the Wasatch Plateau in 1989 and 1990. SSH, EEH = south and east side Heliotrope Mountain, respectively; HMS = head of Mill Stream, Ferron Mountain.

	SSH			EEH			HMS		
	Asmo	Aske	Asmi	Asmo	Aske	Asmi	Asmo	Aske	Asmi
1989									
Hours	24	8	10	30	24	22	8	16	16
Individuals	28	9	10	30	19	10	5	11	18
Individuals/hour	1.2	1.1	1.0	1.0	0.8	0.5	0.6	0.7	1.1
Species	7	3	5	7	7	3	3	4	7
1990									
Hours	30	15	15	12	12	—	12	—	12
Individuals	57	7	35	40	24	—	16	—	24
Individuals/hour	1.9	0.5	2.3	3.3	2.0	—	1.3	—	2.0
Species	10	5	11	5	5	—	6	—	3

when categorized by site and *Astragalus* species visited, six of seven categories had more individuals per hour in 1990 than in 1989.

The initial hypothesis, that *A. montii* would have fewer individual flower visitors than would its common congeners, received little support (Table 1, Appendices I, II). In 1989 there was little difference among species in visitors per person hour at SSH. At EEH *A. montii* flowers were visited more often than the other species. Conversely, at HMS *A. montii* flowers received the fewest visits. In 1990 comparisons of number of visitors among all three *Astragalus* species could be made only at the SSH site where *A. montii* had an intermediate number of visitors per hour. At EEH, *A. montii* again had more visits per hour than *A. kentrophyta*, and at HMS it had fewer visits per hour than *A. miser*.

The prediction that species richness and species diversity of bees visiting the three *Astragalus* species would be lowest for *A. montii* was also provisionally rejected. The number of species captured on *A. montii* commonly exceeded those captured on the other species, both when more hours were spent collecting from *A. montii* than the other species (1989 SSH) and when collecting hours were equal (1990 HMS; Table 1). Only once, when fewer hours were spent collecting on *A. montii* than on the other *Astragalus* species (1989 HMS), was *A. montii* visited by the fewest species of bees. When all sites were considered, total number of species collected on *A. montii* in 1989 exceeded those captured on *A. kentrophyta* and equaled those captured on *A. miser* (Table 2). In 1990 more species were caught

visiting *A. montii* than the other two species, but this difference is probably because we collected at three sites for *A. montii* but at only two for each of the other two species.

Calculations using species diversity, D', also failed to yield expected trends (Table 2). In 1989 diversity of visitors to flowers of *A. montii* was very similar to diversity recorded for *A. kentrophyta* and *A. miser*. Comparisons for 1990 are more tenuous because of the differences among species in number of sites sampled. However, diversity of flower visitors was highest for *A. miser* and similar for *A. montii* and *A. kentrophyta*. Diversity in 1990 was generally lower than in 1989, although number of individuals captured was greater.

The most frequent visitors to these *Astragalus* species in both 1989 and 1990 were *Osmia* bees (Table 3). For the small-flowered *A. montii* and *A. kentrophyta*, in both years >70.0% of all visitors were *Osmia* bees. Only for *A. miser* in 1990 did the percent *Osmia* visitors drop below 50%. *A. miser* was more frequently visited by bumblebees, especially at SSH. The abundance of bumblebees caused SSH to have the lowest percentage of *Osmia* individuals recorded at any site in both years. Even so, *Osmia* bees were always more than 60% of the total flower visitor fauna recorded in any site-year.

Because of greater similarities in flower size, color, and microclimate, we expected *A. montii* and *A. kentrophyta* to have more visitors in common than either did with *A. miser*. This was not true in either year. The three pairings of *Astragalus* did not differ much in the number of bee species they shared, though results

TABLE 2. Number of individuals, number of species, and species diversity (D) of bees found visiting three species of *Astragalus* at three sites on the Wasatch Plateau. In 1989 collections were made for each species at all three sites; in 1990 collections were made at all sites for *A. montii*, but at only two sites for the other two species. For comparative purposes, collection data for the latter two species are shown in 1989 for all three sites and for only the two sites collected at in 1990. D = Simpson's diversity index.

<i>Astragalus</i> species	Individuals		Species		D ¹	
	3 sites	2 sites	3 sites	2 sites	3 sites	2 sites
1989						
<i>montii</i>	63	—	13	—	0.87	—
<i>kentrophyta</i>	39	28	9	8	0.79	0.81
<i>miser</i>	38	28	13	11	0.88	0.87
1990						
<i>montii</i>	113	—	13	—	0.62	—
<i>kentrophyta</i>	—	31	—	7	—	0.60
<i>miser</i>	—	59	—	12	—	0.79

¹In 1989 only individuals that were collected were used in calculations, because uncaptured *Osmia* individuals were not identifiable to species.

TABLE 3. Percent visitors that were *Osmia* bees to the flowers of three *Astragalus* species (abbreviations as in Table 1). Data shown grouped by species across sites, and by site across species, for 2 yr. For comparative purposes, 1989 data are shown in entirety (3 sites or 3 species) or only for the 2 sites or 2 species sampled in 1990.

	Asmo	Aske	Asmi	SSH	EEH	HMS
----- Across sites -----					----- Across species -----	
1989						
3 (sites/species)	88.9	71.8	73.7	62.3	88.1	76.5
2 (sites/species)	—	78.6	64.3	—	85.7	87.0
1990	93.8	74.2	47.5	62.6	87.5	95.0

varied somewhat with year and with index used (Table 4). In 1989 the three pairings of *Astragalus* species had about the same number of bee species in common. In 1990 *A. miser* and *A. montii* had about twice the number of species in common as did the other pairings. Neither coefficient of similarity, C_s or C_i , consistently supported the hypothesis; in 1989, but not 1990, C_s and C_i were highest for the *A. montii*-*A. kentrophyta* comparison.

Many bees visiting *Astragalus* flowers carried pollen on their bodies: 43% of the bees captured, primarily females of the genus *Osmia*, had been collecting pollen. Pollen loads comprised primarily *Astragalus* pollen (all means >80%; Table 5). It is unknown whether loads commonly contained more than one species of *Astragalus* because pollen grains could not be distinguished to species with the light microscope.

Our observations of foraging bees suggest some interspecific movement. In 1989 few *Osmia* individuals flew between *A. montii* and *A. miser* or *A. kentrophyta*; of 74 interplant

movements only two were interspecific. In 1990, 4 of 21 observed interplant movements were between species. Interspecific visits occurred most commonly where species grew intermingled.

DISCUSSION

Two hypotheses make predictions about the abundance and diversity of visitors to the flowers of rare plants. For entomophilous plants, Levin and Anderson (1970), Straw (1972), and Karron (1987) proposed that pollinators should be more flower constant to abundant plant species than to rare ones, that this differential flower constancy would result in more successful reproduction by "majority" species than by "minority" species, and that over time minority species would become extinct because of dwindling recruitment or would evolve some method of self-reproduction (Levin 1972). A corollary of this hypothesis is that both the number and diversity of visitors to the flowers of rare plants should be lower than they are to abundant ones.

TABLE 4. Number of bee species (S) collected on each *Astragalus* species, and number of species shared (C) and similarity indices for each pairing for each year. C_s = Czekanowski's similarity index for bee species presence-absence; C_i = index weighted by individuals captured.

<i>Astragalus</i> species pair	1989				1990			
	S	C	C_s	C_i	S	C	C_s	C_i
<i>montii</i>	13	6	0.50	0.34	13	7	0.56	0.37
<i>miser</i>	13				12			
<i>montii</i>	13	6	0.55	0.43	13	4	0.40	0.35
<i>kentrophyta</i>	9				7			
<i>kentrophyta</i>	13	5	0.45	0.43	12	3	0.32	0.53
<i>miser</i>	9				7			
All three species	20	4	0.35	0.27	21	3	0.28	0.30

In contrast, the facilitation hypothesis (reviewed by Rathcke 1983) predicts that rare species growing with attractive, more abundant species may actually reproduce more successfully because the latter draw many more pollinating insects into the area than would otherwise be present. If so, rare and abundant sympatric species should have similar visitor diversity, and visitor abundances should reflect respective frequencies of the plants. This study indirectly assessed the importance of facilitation and competition. A direct assessment is difficult because (1) the experiments necessary to distinguish between alternatives cannot be conducted when the "plant protagonist" is protected by the Endangered Species Act; and (2) *A. montii* did not occur in the absence of its congeners on our study sites, so visitation rates of "facilitated" and "unfacilitated" populations could not be compared.

Our results supply consistent, though indirect, support for the facilitation hypothesis. Except for bumblebees, which foraged almost exclusively from large-flowered *A. miser*, bees did not discriminate against *A. montii* but rather seemed to treat all three *Astragalus* species as one taxa. First, *A. montii* did not consistently attract fewer visitors per hour than did the other species. Indeed, visitation rates to *A. montii* were higher than to the other species in three of six site-years (Table 1). Second, neither species richness nor species diversity of pollinators was consistently lower for *A. montii* than for the other species (Table 2). In fact, an equal or greater number of species visited *A. montii* than visited the others in both years. And finally, bees were observed moving between species on individual foraging

trips. Gross (1992) also reported that bees foraging on closely related legumes commonly moved between species. Thus, there was no detectable rare species disadvantage and no evidence that endemics, at least those growing in close proximity to abundant congeners, are pollinator-vulnerable.

The shared microhabitat and similarities in flower size and morphology of *A. montii* and *A. kentrophyta* led us to expect that facilitation would be more likely between these two species and, therefore, that they would have more visitors in common than either would with *A. miser*. For example, Thomson (1978, 1981, 1982) found that, in two-species mixtures, the degree of intermingling and the similarity in structure and appearance of congeners' flowers determined the importance of competition and mutualism. The more similar the flowers, the more likely that visitation rates to rare species would be bolstered by the presence of abundant species and the more likely that visitors would be shared. Our data supported this expectation for 1989 but not for 1990 (Table 4). In 1990 C_s for the *A. montii*-*A. kentrophyta* comparison was intermediate to the other comparisons; for C_i it was lower than the other comparisons. Thus, results for the similarity analyses also tend to support the hypothesis that most bees do not distinguish among these *Astragalus* species when foraging, and that the *Astragalus* species tend to facilitate each other's visitation rates.

Only bumblebees seem uninfluenced by *Astragalus* flowers in the aggregate. They clearly preferred flowers of *A. miser* and avoided those of the other *Astragalus* species. Flowers of *A. miser* are large, probably more rewarding, and provide a landing platform from

TABLE 5. Percent *Astragalus* pollen grains in pollen loads, and location of pollen loads carried by bees collected on three *Astragalus* species at three sites on the Wasatch Plateau in 1989 and 1990.

<i>Astragalus</i> species	Number of pollen loads	Mean % <i>Astragalus</i> pollen (+SE)	Location of pollen	
			Abdomen	Legs
<i>montii</i>	45	82 ± 4	42	3
<i>miser</i>	19	90 ± 1	19	—
<i>kentrophyta</i>	5	95 ± 1	5	—

which large, energy-demanding bumblebees can readily forage. Other large-flowered *Astragalus* species also attract numerous large bees such as bumblebees (*Bombus* spp.) and anthophorids (Green and Bohart 1975, Sugden 1985, Karron 1987). In comparison, bumblebees seemed unable to land on the small, weakly supported *A. montii* flowers which are borne above the foliage; they did occasionally exploit the tiny *A. kentrophyta* blossoms while perched on the foliage of that cushion plant.

Factors other than flower abundance can influence the flight path of foraging bees. Because bees are central-place foragers (Orians and Pearson 1979), travel time and energy expended between flower patches and nest are also important. Thus, bees may patronize a flower patch because of its proximity to their nest, even though flowers are more abundant elsewhere. For example, *Osmia* bees mated and nested at the sheltered EEH site where relatively few *A. kentrophyta* or *A. miser* plants grew; the population of *A. montii* was small but dense. Nevertheless, bees visited flowers at least as frequently at EEH as at the other, more flower-rich, sites (Tables 1, 2). Thus, suitability of nesting habitat at EEH, rather than *Astragalus* flower abundance, may best account for the abundance of bees there. The effect of wild bee nesting sites on seed production of surrounding vegetation is poorly studied and warrants additional attention.

Rigorous subalpine communities of the Wasatch Plateau, with frequent high winds, thunderstorms, and below-freezing temperatures during the blooming season, support a surprisingly rich bee fauna. In 2 yr we collected 27+ bee species foraging on *Astragalus* flowers during 2–3 wk (Appendices I, II). These bees are invaluable pollinators of native plants both rare and common. Their welfare must also be considered in management plans for rare

plants. Land managers must eliminate losses of bees to insecticide applications made for rangeland grasshoppers and minimize physical damage to nest sites. The present insecticide-free buffer zone (currently 4.8 km) around rare plant populations should continue to be maintained. Areas where bees nest in soil should also be protected from livestock trampling, off-road vehicle use, and foot traffic (Sugden 1985). Such diversity, comparable to or greater than that of other subalpine areas in North America (Moldenke and Lincoln 1979), is to be marveled at and preserved.

ACKNOWLEDGMENTS

We are grateful to the many people who assisted in this study. Etta Sechrest and Mike Cram were reliable field and laboratory assistants. John Healey, Don Riddle, and Bob Thompson of the U.S. Forest Service and Larry England, U.S. Fish and Wildlife Service, helped in a variety of ways, from locating plant populations to putting a roof over our heads. The manuscript was constructively reviewed by M. Barkworth, K. Harper, and E. Sugden. This study was funded as part of the APHIS Grasshopper IPM Project. It is Journal Paper #4436 from the Utah Agricultural Experiment Station.

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Received 29 April 1993

Accepted 2 June 1994

APPENDIX I. Species of bees collected and observed visiting flowers of *A. montii* (Asmo), *A. miser* (Asmi), or *A. kentrophyta* (Aske) at three sites in 1989. Entries represent number of males/females collected. Observations are in parentheses. Site abbreviations as in Table 1.

Bee species	SSII 1–21 June			EEH 14–25 June			HMS 14–22 June		
	Asmo	Aske	Asmi	Asmo	Aske	Asmi	Asmo	Aske	Asmi
ANDRENIDAE									
<i>Andrena transnigra</i> Vier.	0/1								
<i>Andrena</i> spp.				(1)					

APPENDIX I. Continued.

Bee species	SSH 1-21 June			EEH 14-25 June			HMS 14-22 June		
	Asmo	Aske	Asmi	Asmo	Aske	Asmi	Asmo	Aske	Asmi
APIDAE									
<i>Bombus bifarius</i> Cr.			0/1						
<i>Bombus flavifrons</i> Cr.			(0/2)						
<i>Bombus huntii</i> Greene			(0/2)						0/2
<i>Bombus nevadensis</i> Cr.			0/1						
HALICTIDAE									
<i>Eylaeus niger</i> (Viereck)	0/1								0/1
MEGACHILIDAE									
<i>Anthidium tenuiflorae</i> Ckll.	(2)1/0			(1)	(1)1/2(1)				1/2(2)
<i>Megachile</i> spp.	(1/0)		(1/0)						
<i>Osmia cyanopoda</i> Ckll.		1/0							
<i>Osmia hirta</i> White	0/1								
<i>Osmia longula</i> Cr.									0/1
<i>Osmia nigritrons</i> Cr.		0/1		0/4	0/2				0/3
<i>Osmia aff. nigritrons</i>	0/3						0/1	0/1	
<i>Osmia paradisaea</i> Sanh.				1/0					2/2
<i>Osmia penstemonis</i> Ckll.				0/1					
<i>Osmia pikei</i> Ckll.						0/1			
<i>Osmia pusilla</i> Cr.					0/1				1/0
<i>Osmia sladeni</i> Sanh.		2/0		1/0	4/0	3/0		2/0	
<i>Osmia sladeni</i> &/or <i>alpestris</i>				0/2	0/3	0/2	0/1	0/2	0/5
<i>Osmia tanneri</i> Sanh.	1/3			1/2	0/1	0/1			
<i>Osmia</i> spp.	(5/9)	(1/4)	(0/3)	(8/9)	(1/1)	(1/3)	(1/1)	(0/1)	(0/1)

APPENDIX II. Species of bees collected and observed visiting flowers of *A. montii* (Asmo) at three sites and *A. miser* (Asmi) and *A. kentrophyta* (Aske) at two sites each in 1990. Entries represent number of males/females collected. Observations are in parentheses. Site abbreviations as in Table 1.

Visitor	SSH 19 June-4 July			EEH 19-29 June		HMS 21-29 June	
	Asmo	Aske	Asmi	Asmo	Aske	Asmo	Asmi
ANDRENIDAE							
<i>Andrena nigrihirta</i> (Ashm)			0/1				
<i>Andrena transnigra</i> Vier.	0/1						
APIDAE							
<i>Apis mellifera</i> L.				0/1(5)			
<i>Bombus bifarius</i> Cr.				0/1			
<i>Bombus flavifrons</i> Cr.	0/1	0/1					
<i>Bombus huntii</i> Greene				0/3(6)			
<i>Bombus nevadensis</i> Cr.				0/3(5)			
MEGACHILIDAE							
<i>Anthidium tenuiflorae</i> Ckll.	1/0(2)		2/0			0/1(3)	
<i>Hoplitis fulgida</i> Cr.					3/0		
<i>Megacile melanophaea</i> Smith			2/0				1/0
<i>Megachile perihirta</i> Ckll.	1/0		1/0				1/0

APPENDIX II. Continued.

Visitor	SSH 19 June-4 July			EEH 19-29 June		HMS 21-29 June	
	Asmo	Aske	Asmi	Asmo	Aske	Asmo	Asmi
MEGACHILIDAE (continued)							
<i>Osmia longula</i> Cr.				2/0			
<i>Osmia montana</i> Cr.					1/0		
<i>Osmia aff. nigritrons</i>	0/1		0/1				
<i>Osmia paradisica</i> Sanh.	1/0		0/2	3/0		1/2	
<i>Osmia penstemonis</i> Ckll.						0/1	1/0
<i>Osmia pusilla</i> Cr.		0/1					
<i>Osmia sculleni</i> Ckll.	2/0			1/0			
<i>Osmia sladoni</i> Sanh.	19/13	4/0	1/0	8/16	7/8	3/6	1/21
<i>Osmia subaustralis</i> Ckll.	4/0					1/0	
<i>Osmia tanneri</i> Sanh.	9/2	1/0	1/0	9/1	1/0	0/1	